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THE LAW OF ADAPTIVE RADIATION.

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ONE of the essential features of divergent evolution as conceived in the branching system successively developed by Lamarck, Darwin, Huxley, and Cope has been termed by the writer "adaptive radiation." This term seems to express most clearly the idea of differentiation of habit in several directions from a primitive type, as shown in the accompanying diagrams. The law is a familiar one; it results in the formation of analogous radii in different groups of animals. The first comprehensive illustration of the law known to the writer is that under the headings "Homologous Groups" and "Heterology," in Cope's paper of 1868 on the "Origin of Genera," reprinted in the *Origin of the Fittest* (pp. 95–106). This brilliant essay is marred only by great confusion in the use of terms; but the parallelisms in unrelated groups of amphibians and of mammals such as marsupials and placentals, as first observed by Owen, are clearly brought out.

In the present paper citations from earlier essays of my own may be given bearing upon *general adaptive radiation* and the independent production of analogous radii under the convergent

principles of homoplasy, parallelism, and convergence, which, as shown in the last number of the *Naturalist*, are by no means synonymous terms or identical processes. The altogether similar law of *local adaptive radiation* or incipient divergence on a smaller scale in a single locality may now be more clearly developed.

This idea of radiation becomes a means of interpretation, and a way of imagining the relations of extinct and living faunæ. As perceived by Cope, it applies both on a small and on a vast scale.

I. General Radiation.

In the "Rise of the Mammalia" ('**93**, pp. 30–33) the ancient Mesozoic (Meseutheria) and modern Cenozoic (Ceneutheria) differentiation of the placentals (Eutheria) was spoken of as follows:

The Puerco is essentially an archaic fauna, and is to be regarded as the climax of the first period of placental differentiation, a culmination of the first attempts of nature to establish insectivorous, carnivorous, and herbivorous groups. These attempts began in the Cretaceous, and some of the types thus produced died out in the Puerco, some in the Wasatch and Bridger; only a few flesh-eaters survive to the Miocene. It is most important to grasp clearly the idea of this *functional radiation* in all directions of this old Puerco fauna, resulting in forms like the modern insectivores, rodents, bears, dogs and cats, monkeys, sloths, bunodont and selenodont ungulates, and lophodont ungulates. This was an independent radiation of placentals, like the Australian radiation of marsupials.

Some of the least specialized spurs of this radiation appear to have survived and become the centers of the second or mid-Tertiary radiation, from which our modern fauna has evolved. Yet we have not in a single case succeeded in tracing the direct connection.[1] To sum up, we find on the North American continent evidence of the rise and decline and disappearance of monotremes and marsupials, and two great periods of placental radiation, the *ancient radiation* beginning in the Mesozoic, reaching a climax in the Puerco and unknown post-Puerco, and sending its spurs into the higher Tertiary, and the *modern radiation* reaching its climax in the Miocene, and sending down to us our existing types.

[1] This statement has been modified by subsequent discovery.

In the "Origin of the Mammals" ('99, p. 92) the idea was developed as follows:

To guide our speculation in the unknown pre-Tertiary period, we may gather certain positive principles from the known evolution of the Tertiary Mammalia. First, we know that *adaptive radiation*, characteristic of all vertebrates, and beautifully illustrated among Reptilia, is in a very high degree distinctive of Mammalia, because of their superior plasticity.

The *focal-types*, or most primitive forms of the radiations, I–IV, *were certainly small, terrestrial, clawed, insectivorous or omnivorous forms.* It is noteworthy that in the evolution of each radiation, so far as we know at present, land types and organs are invariably primitive, and water types and organs are secondary, exactly as we find among the Reptilia. In fact, we have not found a single instance in which a mammal or reptile series is known to be transformed from a water into a land type; it is always the reverse. There is certainly no evidence for a cetoid (Albrecht) stem of the Mammals. Again, it is obvious that neither carnivorous nor herbivorous types with highly specialized or reduced teeth and feet can be so central as insectivorous and omnivorous types. In fact, the Insectivores among Placentals, and Opossums among Marsupials, are the only animals which have preserved the dental prototype close to that of the Promammal.

The radiations spoken of in this essay were:

I. *Marsupial Radiation of Australia* (Meteutheria).
II. *Tertiary Placental Radiation of the Northern Hemisphere*, i.e., *North America, Asia, and Europe* (Ceneutheria).
III. *Tertiary Placental Radiation of South America* (Ceneutheria).
IV. *Cretaceous Placental Radiation of North America* (Meseutheria).
V. *Jurassic Radiation of Placentals and Marsupials.*

In a subsequent paper, "The Geological and Faunal Relations of Europe and America during the Tertiary Period, and the Theory of the Successive Invasions of an African Fauna" ('00), the subject was further developed as follows:

Now it is a well-known principle of zoölogical evolution that an isolated region, if large and sufficiently varied in its topography, soil, climate, and vegetation, will give rise to a diversified fauna according to the law of adaptive radiation from primitive and central types. Branches will spring off in all directions to take advantage of every possible opportunity of securing food. The modifications which animals undergo in this adaptive radiation are largely of mechanical nature, they are limited in number

and kind by hereditary, stirp, or germinal influences, and thus result in the independent evolution of similar types in widely separated regions under the *law of parallelism or homoplasy*.[1]

II. Adaptive Radiation of Orders and Families as bearing on Geographical Distribution.

This law causes the independent origin not only of similar genera but of similar families and even of similar orders. Nature thus repeats herself on a vast scale, but the similarity is never complete or exact. When migrations are favored by over-population or geographical changes, a new and severe test of fitness arises by the mingling and competition of the parallel types.

Under the operation of these laws a most interesting generalization or hypothesis can be made as to the three [zoölogical] realms: geographical

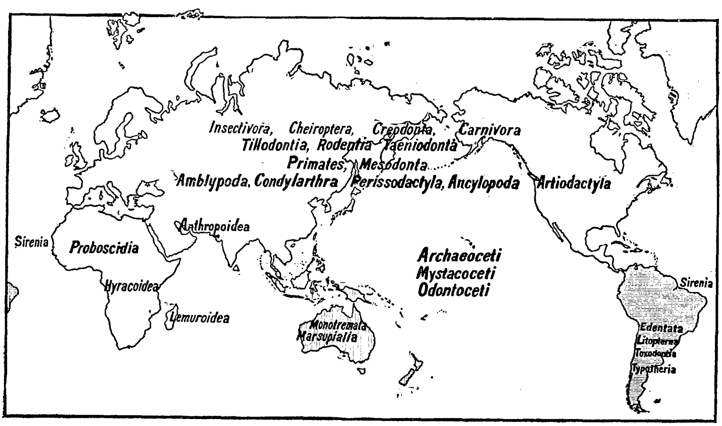

FIG. 1. — Orders of mammals placed in their hypothetical chief centers of adaptive radiation during the Tertiary period. (From Osborn.)

isolation has been so continuous and prolonged that great orders of mammals have been evolved . . . in each. Thus *Arctogæa*, containing the broadest and most highly diversified land area, appears hypothetically as the center in which fourteen primitive and specialized orders radiated from each other. In the southern portion of *Neogæa* at least four orders sprang from primitive members of the above orders, and the Hystricomorph rodents enjoyed their chief radiation. In *Notogæa* two orders were cut off by the sea; one of them a rapidly declining type, the Monotremes, the other, the Marsupials, enjoying a very highly diversified radiation. This

[1] At this time the distinction between homoplasy and parallelism was not appreciated by the writer.

hypothesis is expressed in Fig. III [Fig. 1]. The other orders of mammals, the Sirenia (probably a branch of the hoofed tribe), took the rivers and coasts of America, Europe, and probably Africa as their radiating center, while the Cetacea occupied the fourth or oceanic realm.

We mean to express by this hypothesis that REALMS [Fig. 2] *were the main centers of adaptive radiation of orders of mammals*, but by no

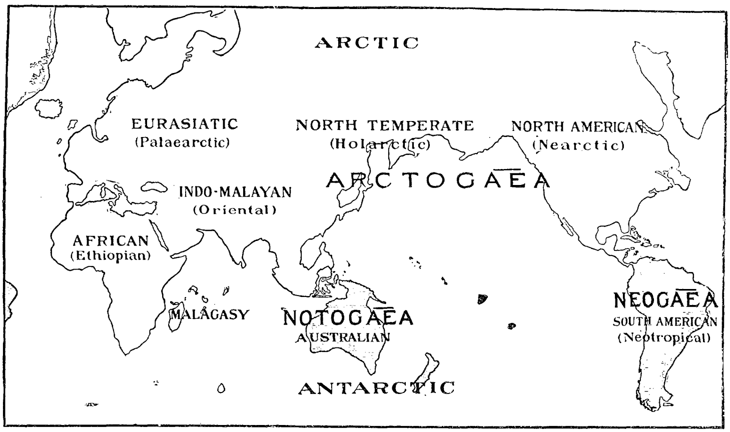

FIG. 2.— Division of the world into three realms and nine main geographical regions. The continental platform is raised to the 200 meter line showing the main Tertiary land connections. (From Osborn.)

means the exclusive areas of distribution, for during the periods of land contact certain members of these orders found their way into adjacent realms. Each realm, therefore, contains its pure autochthonous types and its migrant or derived types. REGIONS, on the other hand, may be distinguished from realms as geographical and zoölogical areas, which have been isolated from each other for shorter periods, either by climatic barriers, as in the case of the Arctic or circumpolar region, or by great physical barriers, such as masses of water and of desert sands. In certain cases these regions, such as Africa, appear to have been so large, distinct and isolated, as to have become important centers of the radiation of certain *orders* of mammals and almost attain the rank of realms, but regions in general are chiefly and permanently distinguished by the *adaptive radiation of families of mammals.*

In this paper Africa was treated hypothetically as a great center of independent evolution and as the source of successive northward migrations of animals. This hypothesis has recently been confirmed by remarkable paleontological discoveries in northern Africa. This adds to the above list of five radiations a sixth, namely:

VI. *African Radiation of Placentals*, chiefly Proboscidea; Hyracoidea; the families Antelopidæ, Giraffidæ, Hippopotamidæ, etc.

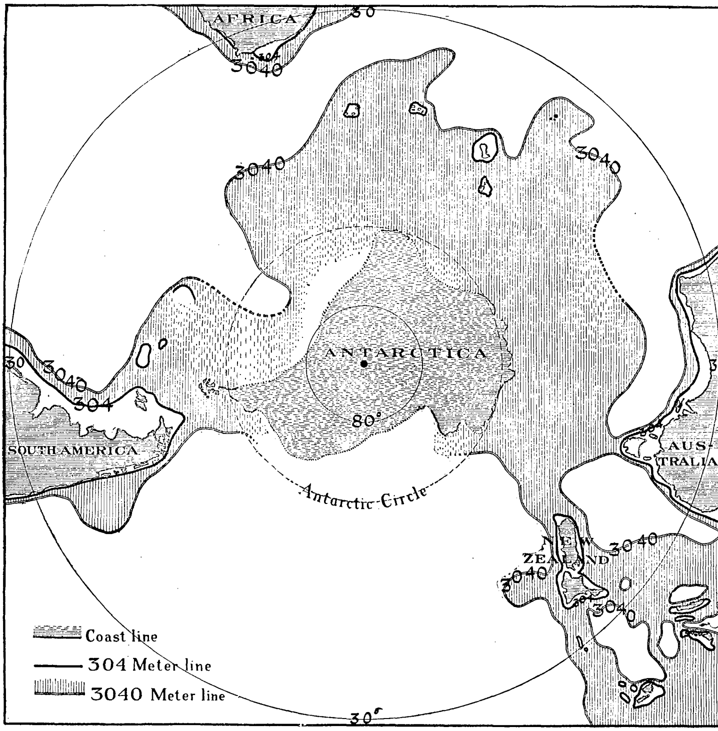

Fig. 3.— Restoration of Antarctica, a hypothetical center of Tertiary adaptive radiation, by elevation to the 3040 sounding line, showing old continental lines. (From Osborn.)

III. The Law of Local Adaptive Radiation as exhibited in Related Contemporaneous Types.

As seen in operation among the ungulates the competition and range for food originates the lengthening of limb from slow-footed into cursorial types, and the lengthening of teeth from short-crowned (brachyodont) into long-crowned (hypsodont) types, and frequently the lengthening of skull from brachycephalic into dolichocephalic types (Osborn, '02a).

The especial application to paleontology to be noted here is that as these types may have lived together or in proximity and resorted to the same water courses for drink, their fossilized

remains are often found together. Yet if we examine analogous types living to-day, we see that they do not frequent exactly the same feeding ranges nor do they subsist upon exactly the same food; they thus do not compete. Good illustrations of this *local adaptive radiation* are seen in the distribution in Africa of the closely allied square-lipped *Rhinoceros simus* with hypsodont teeth, which lives upon grasses, and the more pointed-lipped *R. bicornis* with brachyodont teeth, which lives mainly upon shrubs. Both species belong to the same phylum of rhinoceroses. Among fossil types closely related to the above we observe similar cases, such as the coexistence in the lower Pleistocene of the hypsodont *R. antiquitatis* (woolly rhinoceros) and the brachyodont *R. hemitœchus.*

If carried farther than in the above instances, we may be justified in placing these *local adaptive radiations* in separate subfamilies, because in many cases they give rise to distinct and long-persistent collateral phyla.

Examples of this kind are numerous among the ancient Perissodactyla or ungulates related to the horses, tapirs, and rhinoceroses, as seen below.

	I. STOUT-FOOTED, HEAVY-LIMBED PHYLUM.	II. SLENDER-FOOTED, LIGHT-LIMBED, CURSORIAL PHYLUM.
Families.	*Subfamilies.*	*Subfamilies.*
1. Palæotheriidæ	Palæotheriinæ *B.*[1] (Middle Eocene to Lower Oligocene)	Palaplotheriinæ (Middle Eocene to Lower Oligocene)
2. Titanotheriidæ	Palæosyopinæ *B.* (Middle Eocene to Upper Eocene)	Telmatototheriinæ *H.*[1] (Middle Eocene to Upper Eocene)
3. Hyracodontidæ	Hyrachyinæ *B.* (Middle to Upper Eocene)	Triplopodinæ *B.* (Middle to Upper Eocene)
4. Lophiodontidæ	Lophiodontinæ *B.* (Middle to Upper Eocene)	Helaletinæ *B.* (Eocene) Colodontinæ *B.* (Oligocene)

It will be observed at once that there is no inherent correlation between *brachyodontism* and *brachypody*, or *hypsodontism* and *dolichopody*, or elongation of the feet, as we might have anticipated, although hypsodontism is gradually developed in

[1] B. = brachyodont; H. = hypsodont.

most long-footed series because subsistence upon grasses is associated with such conditions of life as are afforded by extensive open plains, long ranges for food, and rapid flight from enemies. Again, as shown elsewhere, dolichocephaly and dolichopody, brachycephaly and brachypody are frequently but not invariably correlated. (See Osborn, '02a.)

The value of this law of *local adaptive radiation* is especially great as a means of interpretation of the frequent contemporaneous existence or association of more primitive (brachyodont) with more specialized (hypsodont) types. Among Tertiary machærodont cats it is seen in the contemporary long-limbed *Dinictis* and short-limbed *Hoplophoneus*. In fact, the association has been so often observed that if we find one phylum, we may almost anticipate or predict the discovery of the other.

The law is made more clear by referring to the above table and the following explanation of it: (1) As compared with the Palæotheriinæ, the Palaplotheriinæ are so long-footed that Huxley believed that they gave rise to the horse, and he actually placed *Paloplotherium minus* as the ancestor of the horse series. (2) The Telmatotheriinæ are large animals also distinguished by very long, slender limbs; they independently acquired horns, and the species *T. cornutum* was believed by Osborn to be ancestral to the titanotheres; but as a matter of fact, as shown by Earle and Hatcher, this horn is a pure case of parallelism, since the titanotheres probably sprang from the short-skulled and relatively stout species, *Palæosyops manteoceras*, a member of the Palæosyopinæ. (3) The Triplopodinæ present the most extreme instance of light-limbed development among the perissodactyl ungulates, since the limbs have the proportions of some of the most slender and swift-footed ruminant mammals, although these animals are found in the same beds with the correlated subfamily Hyrachyinæ. (4) Among the Lophiodontidæ, the Helaletinæ bring out with additional force the principle that this elongation of limb occurred at a very early geological period; because the first known member of this phylum appears way down in the Lower Eocene, Wasatch, or Suessonien beds, in the genus *Heptodon* Cope, a remarkably light-limbed form, and it runs right through,

so far as we know, into the Oligocene genus *Colodon*, the three-toed type with extraordinarily elongate digits. So far as we know, this light-limbed series is found both in America and Europe, while the heavy-limbed Lophiodontinæ are found only in Europe.

Since the above was written the titanotheres have been more carefully examined by the writer (Osborn, '02b), and, like the rhinoceroses, they are found to subdivide into four contemporaneous phyla distinguished chiefly by dolichocephaly and brachycephaly and by relatively long and short limbs, thus affording another conspicuous illustration of this *law of local adaptive radiation*.

IV. Radiation and Correlation of Structure.

In the careful consideration of adaptive radiation from certain stem types is to be found the true significance of Cuvier's *law of correlation* as modified by the — to him — unknown principle of evolution. Referring to the diagrams, Fig. 4, two important principles are brought out: First, practically all the adaptations known among mammals have arisen by combinations of divergence independently pursued in the limbs and teeth; for example, an herbivorous tooth type may combine with a terrestrial, arboreal, or volant limb type, according as the search for plant food is on the earth, in the trees, or in the air. Although every imaginable combination (*e.g.*, aquatic limbs, myrmecophagous dentition) cannot be realized, yet these combinations have been multiplied almost *ad infinitum* and constitute the fatal defect of Cuvier's law as he conceived it. As tested by a single case, the Eocene monkeys of the family Notharctidæ acquired teeth exactly homoplastic with those of Eocene horses, but the former were provided with arboreal, the latter with terrestrial, limb types. Second, correlation of limb and tooth structure in a given group is further conditioned by the particular combination and degree of specialization of limbs and teeth which the radiation originates with. For example, the primitive placentals combined tritubercular insectivorous teeth with a generalized or probably terrestrial

type of feet; the Australian marsupial radiation, on the other hand, began with a dental type similar to that of the placentals,

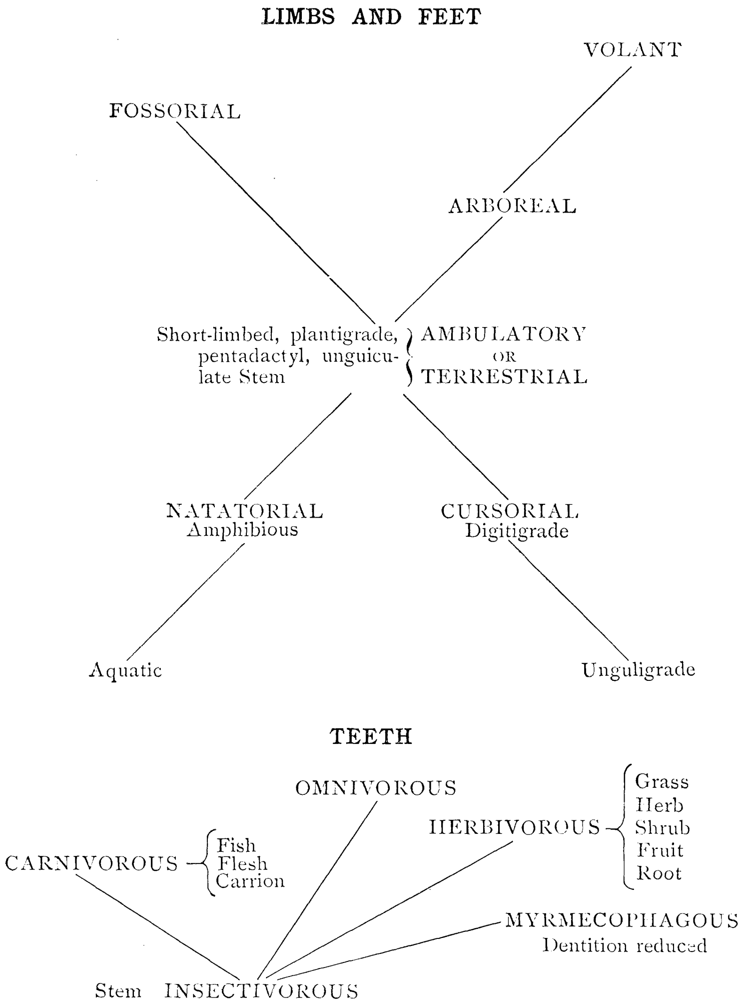

FIG. 4.—Main lines of adaptive radiation of (*a*) limbs and feet, (*b*) teeth among mammals.

but, as Dollo and Bensley have shown, the foot type was of highly specialized arboreal character.

These two fundamental exceptions make clear why it is impossible, as many writers have observed, to reconstruct an

entire animal from either a claw or a tooth. Thus, while the law of correlation is no less dominant than Cuvier supposed, only a vestige is left of the mode of archetypal operation of the law as he conceived it. It may be now restated as follows: Feet (correlated chiefly with limb and body structure) and teeth (correlated chiefly with skull and neck structure) diverge independently in adaptation respectively to securing and eating food under different conditions. Each evolves directly for its own mechanical functions or purposes, yet in such a manner that each subserves the other.

Correlation is therefore not morphological, as Cuvier supposed, but physiological, function always preceding structure. It becomes closest where teeth and feet combine in the same function as in the prehensile canines and claws of the Felidæ, and most diverse where the functions are most diverse, as in the teeth and paddles of the Pinnipedia.

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